

Figures 30–33. Shells of *Ankoravaratra capdambrae* Emberton, gen. & sp. nov. Figure 30. Holotype in three views (UF 285444). Figures 31–33. Paratypes in one view. Figures 31, 32. Male and female, specimens #2 and 1, respectively, from type locality (UF 285446). Figure 33. Male with its operculum in exterior view (UF 285445). Scale bar = 1 mm.

mately 0.89 mm in diameter. Embryonic sculpture smooth. Body-whorl sculpture of "very irregular growth lines, often located on the lower part of the whorl, without reaching the suture. Color "opaque, whitish, with the summit brownish-rosish." No color band.

Distribution: Ankarana Reserve, northern Madagascar.

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LITERATURE CITED

- BEQUAERT, J. & W. J. CLENCH. 1936. Studies of African land and freshwater mollusks. VII. New species of land operculates, with descriptions of a new genus and two new subgenera. *Revue de Zoologie et de Botanique Africaines* 29:97–104, pls. I and II.
- BRUGGEN, A. C. VAN. 1982. A revision of the African operculate land snail genus *Maizaniella* (Gastropoda Prosobranchia: Maizaniidae), with the description of six new taxa. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 85:179–204.
- BRUGGEN, A. C. VAN. 1985. *Neomaizania coryli*, a new genus and species of Maizaniidae (Mollusca Gastropoda Prosobranchia) from Malawi, South Central Africa. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 88:395–403.
- BRUGGEN, A. C. VAN. 1986. Further notes of Afrotropical prosobranch land molluscs (Gastropoda Prosobranchia: Maizaniidae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* 89:357–378.
- BRUGGEN, A. C. VAN. 1990. Notes on the genus *Maizaniella* (Gastropoda, Prosobranchia: Maizaniidae), with the description of a new species from West Africa. *Basteria* 54:187–195.
- EMBERTON, K. C. 2002. *Owengriffithsius* new genus of cyclophorid land snails endemic to northern Madagascar. *The Veliger* 45(3):203–217.
- EMBERTON, K. C. & T. A. PEARCE. 1999. Land caenogastropods from Mounts Mahimana, Ilapiry, and Vasiha, southeastern Madagascar, with conservation statuses of 17 species of *Boucardicus*. *The Veliger* 42:338–372.
- EMBERTON, K. C., T. A. PEARCE & R. RANDALANA. 1996. Quantitatively sampling land-snail species richness in Madagascar rainforests. *Malacologia* 38:203–212.
- FISCHER-PIETTE, E., C. P. BLANC, F. BLANC & F. SALVAT. 1993. *Gastéropodes terrestres prosobranches. Faune de Madagascar* 80:1–281.
- GIRARDI, E.-L. 1978. The Samoan land snail genus *Ostodes* (Mollusca: Prosobranchia: Poteriidae). *The Veliger* 20:191–250.
- MORTON, J. E. 1952. A preliminary study of the land operculate *Murdochia pallidum* (Cyclophoridae, Mesogastropoda). *Transactions of the Royal Society of New Zealand* 80:69–79, pls. 25–26.
- PONDER, W. F. & D. R. LINDBERG. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119: 83–265.
- SOLEM, A. 1959. Systematics and Zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana: Zoology* 43:1–359, pls. 1–34.
- TEMPLETON, A. R. 1989. The meaning of species and specification: a genetic perspective Pp. 3–27 in D. Otte & J. A. Endler (eds.), *Specification and Its Consequences*. Sinauer Associates: Sunderland, Massachusetts.
- THOMPSON, F. G. 1969. Some Mexican and Central American land snails of the family Cyclophoridae. *Zoologica: New York Zoological Society* 54:35–77, pls. 1–VII.
- TIELECKE, H. 1940. Anatomie, Phylogenie und Tiergeographie der Cyclophoriden (aus der Mollusken-Abteilung des Zoologischen Museums der Universität Berlin). *Archiv für Systematische Zoologie, Neue Folge* 9:317–371.
- VAUGHT, K. C. 1989. A Classification of the Living Mollusca. American Malacologists Inc.: Melbourne, Florida.
- VERDCOURT, B. 1963. A new species of *Maizania* from northern Kenya. *Archiv für Molluskenkunde* 92:15–17.
- VERDCOURT, B. 1964. The genus *Maizania* Bgt. (Gastropoda, Maizaniidae) in eastern Africa. *The Journal of the East Africa Natural History Society and Coryndon Museum* 24:1–22.
- WENZ, W. 1938–1944. Gastropoda, Teil 1: Allgemeiner Teil und Prosobranchia. Band 6, Pp. 1–1639 in O. H. Schindewolf (ed.), *Handbuch der Paläozoologie*. Gebrüder Bornträger: Berlin.

Dichotomous Life History Patterns for the Nudibranch *Dendronotus frondosus* (Ascanius, 1774) in the Gulf of Maine

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Abstract. The nudibranch *Dendronotus frondosus* has a wide distribution and different morphological, ecological, and life history traits within its range. In the Gulf of Maine, populations can be found with either lecithotrophic or planktotrophic veliger larvae. Adults with these two types of larvae have overlapping habitat distributions, but the veligers differ in size, basic developmental characteristics, and composition of gelatinous clutches. Seasonal patterns of size distribution of adults suggest a sub-annual life cycle for those with planktotrophic larvae and an annual life cycle for those with lecithotrophic larvae. A feeding experiment with two types of hydroid prey resulted in lower growth rates for one dietary treatment, although this did not result in a shift in larval type. Mating recognition trials suggest a behavioral reproductive isolating mechanism between some populations. These results show little evidence for poecilogony and are motive for a taxonomic review of a *D. frondosus* complex in the Gulf of Maine.

INTRODUCTION

Poecilogony is broadly defined as multiple larval development modes within members of a single species (Hoagland & Robertson, 1988; Levin & Bridges, 1995). Examples of this phenomenon have frequently been shown to be sibling species complexes (Hoagland & Robertson, 1988), and proven examples of poecilogonous marine invertebrates include a limited number of species of spionid polychaetes and opisthobranch gastropods (Levin, 1984; Bouchet, 1989; Krug, 1998). When studying differences in reproductive traits within these groups, the possibility for poecilogony must be examined.

Dendronotus frondosus (Ascanius, 1774) is a cosmopolitan nudibranch in northern temperate coastal waters and one of the most common opisthobranchs in the Gulf of Maine; however, descriptions of the habitat ecology, reproductive ecology, and general morphology of this species vary significantly (Alder & Hancock, 1845–1855; MacFarland, 1966; Robilliard, 1970). For example, a variety of hydroid diets have been associated with *D. frondosus* (McDonald & Nybakken, 1999). With this range of diets follow drastic differences in pigmentation patterns (Robilliard, 1975) and qualitative variation in ceras and foot morphology (personal observation). In addition, life history information varies considerably for reported reproductive season and general developmental characteristics (Swennen, 1961; Clark, 1975; Thompson & Brown, 1984). Because of these varying attributes, over 17 different taxonomic designations have confused the status of *D. frondosus*, as this species continues to be redefined in the literature (Robilliard, 1970; Thollessen, 1998). Reports of this species have been accumulated from Norway, Greenland, the western and eastern North

American coasts, and the northern Asiatic coast (Robilliard, 1970), largely because this species epithet continues to be a general designation for the genus *Dendronotus*.

Dendronotus frondosus feeds on a variety of athecate (e.g., *Tubularia* spp.) and thecate (e.g., *Obelia* spp.) hydroids (Miller, 1961; Swennen, 1961; Todd, 1981), and differences in diet often are coupled with drastic differences in physical habitats and seasonal population fluctuations. In the Gulf of Maine, *D. frondosus* habitats range from southern coastal areas associated with subtidal hydroid communities (Clark, 1975; Lambert, 1991) to the Bay of Fundy and northern Nova Scotia (Meyer, 1971; Bleakney, 1996). Throughout the region these slugs are commonly found in subtidal thecate hydroid communities and fouling communities with athecate hydroid colonies (Meyer, 1971; Clark, 1975; Lambert, 1991). In northern regions of the Gulf of Maine, *D. frondosus* regularly occurs in intertidal habitats associated with the thecate hydroid *Sertularia pumila*, a common rockweed epiphyte (Meyer, 1971; Gionet & Aiken, 1992; Bleakney, 1996).

In the North Atlantic, in addition to variability of habitats, *D. frondosus* shows a range of reproductive patterns. Reports of seasonal spawning vary from strictly annual (Clark, 1975) to nearly year-round (Swennen, 1961). Larval feeding type may also differ; both lecithotrophic (Thompson & Brown, 1984) and planktotrophic larvae (Clark, 1975) have been described for this species on opposite sides of the Atlantic. Hoagland & Robertson (1988) noted that these allopatric differences in life history data warrant further examination for the possibility of poecilogony.

This paper outlines subtidal and intertidal habitats of *D. frondosus* in the Gulf of Maine and describes variation in the larval development and feeding type of this nudi-

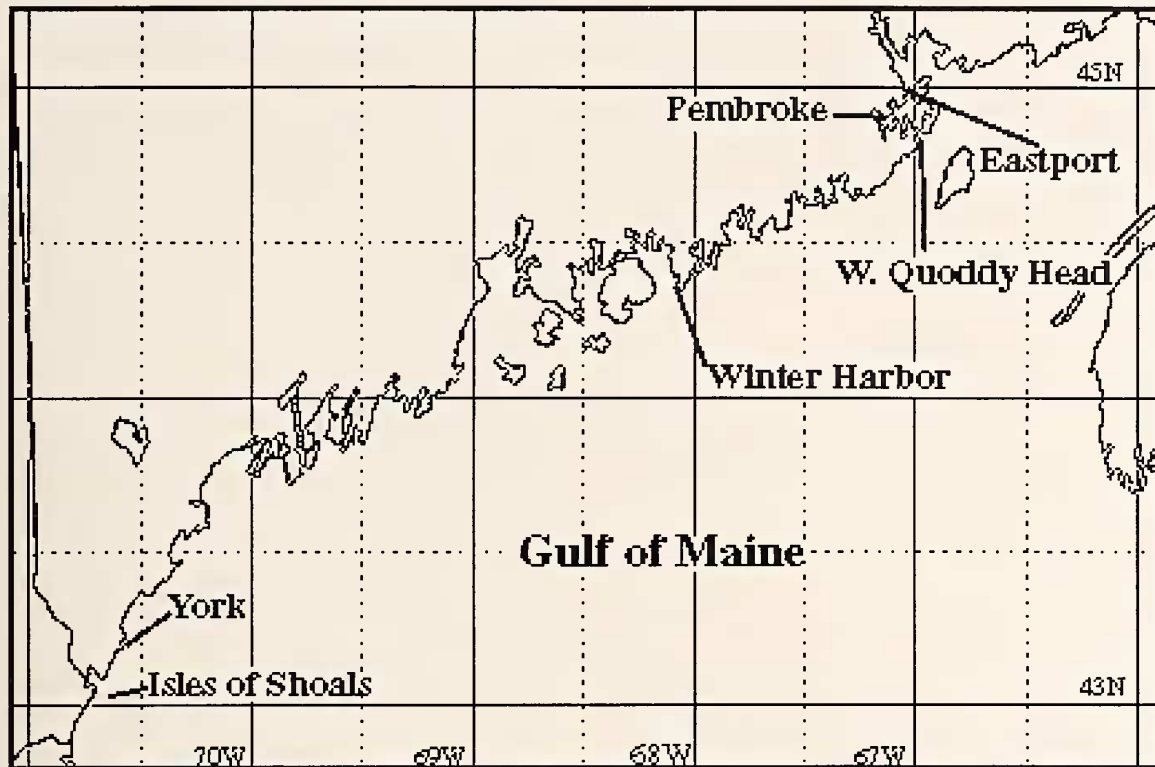


Figure 1. Map of study sites on the Maine and New Hampshire coastline. Southern subtidal sites include York and Isles of Shoals. Northern subtidal sites include Winter Harbor, Eastport, and Pembroke. Northern intertidal sites include Pembroke and West Quoddy Head.

branch associated with differences in habitat ecology. These observations were motive for a simple reciprocal feeding experiment to evaluate the effects of two major diets on the type of larvae produced. A mating recognition experiment provided data on the potential for reproductive isolation of the most disparate groups of *D. frondosus*, although a formal taxonomic review is not included in this paper.

MATERIALS AND METHODS

Collection and Life History Observations

I collected *Dendronotus frondosus* individuals from intertidal and subtidal (5–10 m deep) sites in the Gulf of Maine between March 1997 and August 1998 (Figure 1). Southern subtidal sites were at Cape Neddick in York, Maine (43°00'N, 70°36'W), and at the Isles of Shoals, New Hampshire (44°21'N, 68°03'W). Northern subtidal sites were at Winter Harbor (44°53'N, 67°09'W), Eastport (44°54'N, 66°59'W) and Pembroke (44°53'N, 67°09'W), Maine. Northern intertidal collection sites included Pembroke and West Quoddy Head (44°49'N, 66°57'W), Maine. I monitored these sites three to six times/year to establish seasonal patterns in spawning behavior. Adult *D. frondosus* were maintained in a 10°C temperature-con-

trolled room at the University of New Hampshire (UNH) Durham campus and fed hydroids (*Obelia* spp. and *Sertularia* spp.) found as epiphytes on the rockweed *Ascophyllum nodosum*. Lengths of nudibranchs were measured with an ocular micrometer and a dissecting microscope while the animals were actively crawling on a flat submerged surface.

I isolated individual nudibranchs for 1–2 days at 10°C in order to collect spawn masses when they were deposited. All larval measurements were made with an ocular micrometer ($\pm 10 \mu\text{m}$) and a compound microscope. Zygote diameters were measured by haphazardly selecting 10 zygotes in the center region of different spawn masses. The embryos were then placed in 200 mL plastic-covered containers with natural seawater (32–35 ppt) and gently aerated. I changed the water and culture container two times per week and monitored the development of the embryos until they began to hatch from the capsules and gel matrix of the mass. The number of days until hatching for each spawn mass (± 1 day) was recorded. I then measured the maximum shell length from the aperture just above the velum of three to seven larvae from four spawn masses for each larval type. Immediately after hatching, several larvae were presented with hydroid material (*Obelia* and *Sertularia* spp.) and observed for signs of

induction of metamorphosis such as resorption of the velum and the loss of shell and operculum (Todd, 1981). Planktotrophic and lecithotrophic larvae from four different spawn masses for each type were placed into glass stacking dishes in seawater at approximately one to two veligers/mL. The larvae were maintained at 10°C and fed small amounts of the cultured microalgae, *Isochrysis galbana* and *Rhodomonas salina*. After 1 week of culture, the larvae were examined with a compound light microscope for the presence of algal material in their gut.

Reciprocal Feeding Experiment

Two reciprocal feeding experiments helped me determine the quality of two hydroid diets and the plasticity of the larval types produced by adults fed these diets. I haphazardly collected 60 juvenile *D. frondosus* (12.9–34.5 mm) from northern intertidal sites in October 1997, and placed them in covered plastic containers (18.4 × 16.5 × 11.1 cm) with two opposite mesh windows in flow-through seawater tables at the UNH Coastal Marine Laboratory in Newcastle, New Hampshire. The two dietary treatments were either *Obelia* or *Sertularia* spp. found as epiphytic colonies on *Ascophyllum nodosum* on a nearby pier, fed to the nudibranchs one to two times per week, amounting to an *ad libitum* regime. After 3 months, I measured the remaining 51 individuals (22 fed on *Obelia* spp. and 29 fed on *Sertularia* spp.) and paired them for mating and production of spawn masses. Eleven pairs of nudibranchs from the *Obelia* treatment and 13 pairs fed *Sertularia* spp. were observed as they spawned for 2 months.

A similar experiment used *D. frondosus* from southern subtidal sites with the same feeding and maintenance schedules. Starting lengths ranged from 3.3–16.7 mm for the 72 juveniles collected between March and April 1998. The final measurements were collected after only 4 weeks of growth when mortality reduced the number of survivors to 36 slugs (24 fed *Obelia* spp., 12 fed *Sertularia* spp.). Additional mortality reduced the number of pairs of nudibranchs to 10 pairs for the *Obelia* treatment and five pairs for the *Sertularia* treatment which were observed as they spawned for an additional 2 weeks.

The total number of spawn masses was then recorded and the larvae were allowed to develop until I could distinguish them as either planktotrophic or lecithotrophic larvae. The assessment of these larval types was based on morphological characteristics of the digestive gland, propodium, and shell. Growth data were analyzed using a 2-tailed t-test, and the number of spawn masses between treatments was compared using a Mann-Whitney test for non-parametric data.

Mating Recognition Behavior

Adult slugs between 1.3 and 4.1 cm long were collected in May 1998 from breeding populations at northern

intertidal and southern subtidal sites. I isolated individuals in covered plastic containers (18.4 × 16.5 × 11.1 cm) at 10°C for at least 5 days prior to the experiment. Three treatment groups consisted of 18 pairs of similarly sized slugs (±1.0 cm). Pairs of adults that were both collected from northern intertidal sites composed one treatment group, another used pairs from southern subtidal sites, and the experimental group consisted of one adult *D. frondosus* from each of the two habitats. I checked the pairs every hour during a 7-hour period on the first day and a 4-hour period for another 4 days and recorded the number of pairs engaged in copula. Coupling lasted between 2–7 hours, so this monitoring routine was adequate for recording these mating events. I compared frequency counts of mating between the mixed pairs and either the northern intertidal or southern subtidal pairs using a 2 × 2 contingency table with a Log-likelihood ratio (G-test) and a Yates correction for continuity. In addition, I paired four adults from northern subtidal sites: two with individuals from northern intertidal sites and another two with adults from southern subtidal sites. After observing for mating recognition, I then switched pairings to document the behavior with adults from the other sites (either northern intertidal or southern subtidal).

RESULTS

Habitats and General Characteristics

Southern Subtidal Habitats. *D. frondosus* is found associated with colonies of *Obelia* spp. growing on rocky ledges and as epiphytes on the kelps *Laminaria* spp. and *Agarum cribosum* (Lambert, 1991). Other nudibranchs common to these communities include *Coryphella verrucosa*, *Tergipes tergipes*, and *Doto coronata*. *D. frondosus* at these sites produces only spawn masses with developing planktotrophic larvae. Adult *D. frondosus* commonly had extensive white or dark brown mottling on a reddish brown body.

Northern Intertidal Habitats. *D. frondosus* is found midway through the protected rockweed zone in dense beds of *Ascophyllum nodosum* (Gionet & Aiken, 1992; Bleakney, 1996). Here, these slugs are commonly found eating the epiphytic and epilithic hydroid *Sertularia pumila*. The only other nudibranch frequently found in these habitats is a bryozoan feeder, the dorid *Acanthodoris pilosa*. *D. frondosus* is found in rocky crevices at the base of *A. nodosum*. They deposit spawn masses on the algae and primary substrate, frequently intertwined with the hydroid colonies. Their color is strictly pale white-yellow, with extremely limited mottling on the dorsal side adjacent to the cerata. More colorful *D. frondosus* with extensive mottling can be found infrequently in the littoral zone in southern regions of the Gulf of Maine such as Appledore Island, Maine, but never with the consistency and relatively high densities of those sites in the northern Gulf of Maine. Northern intertidal sites at West Quoddy

Head and Wilbur Neck (Figure 1) always had *D. frondosus* spawn masses that yielded lecithotrophic larvae. No planktotrophic larvae were found in *D. frondosus* masses at these habitats.

Northern Subtidal Habitats. I found *D. frondosus* at subtidal sites in Winter Harbor, Eastport, and Pembroke, Maine (Figure 1) associated with *Obelia* spp. and related thecate hydroids. These slugs were either reddish brown with white and dark mottling or pale purple or white with limited or no mottling. Collected spawn masses produced either lecithotrophic or planktotrophic larvae depending on the time of year of sampling.

Seasonal Spawning and Adult Size Distribution

At two southern subtidal sites, York and the Isles of Shoals, *D. frondosus* had an annual spring spawning event with adults that, when present, were producing spawn masses (Figures 2a, b). After spawning, adult populations senesced and for several months did not occur at these sites (Figures 2a, b). At two northern intertidal sites, West Quoddy Head and Wilbur Neck, *D. frondosus* also had an annual spawning period in the spring or early summer (Figures 2c, d); however, new recruits appeared at these sites a few months after the spawning event and gradually increased in size throughout the fall and winter without depositing spawn masses apparently until the following spring (Figures 2c, d). Note that there was a brief annual period at the Wilbur Neck site when no *D. frondosus* were found (Figure 2d). The two northern intertidal sites were offset in the timing of these patterns of growth and spawning, with Wilbur Neck having an earlier spawning event than West Quoddy Head (Figures 2c, d).

Larval Types and Characteristics

No mixed clutches (i.e., both planktotrophic and lecithotrophic larvae) were found at any of the collection sites. All spawn masses from the two types of *D. frondosus* had one embryo/capsule and each formed a hollow cylindrical capsule-filled cord that was attached along one side, or Type B according to Hurst (1967). All veliger larvae had Type 2 inflated egg-shaped shells (Thompson, 1961).

There were large differences in the zygote size, time spent in the embryonic capsule from deposition to hatching, and in larval shell size at hatching (Table 1). Lecithotrophic larvae began with relatively large zygotes and took approximately a month to hatch. When they did hatch, they were much larger than the planktotrophic larvae with a robust velum, a propodium and a visceral mass that occupied a large amount of the larval shell (Figure 3a). When offered microalgae, none were ingested by these veligers or at least were not immediately present in the larval gut. The lecithotrophic veligers began metamorphosis within a few hours to 1 day of hatching either on the egg mass material or on the hydroids *Obelia* spp.

and *Sertularia* spp. They were never observed metamorphosing within the embryonic capsule.

Planktotrophic veligers originated from smaller zygotes, took less time to hatch (approximately 1 week), and were much smaller upon hatching than their lecithotrophic counterparts (Table 1). These veligers would not metamorphose upon hatching despite the presence of hydroid material. They actively ingested microalgae when offered it, which was apparent by the presence of red and brown material in the larval gut and digestive gland. The planktotrophic larvae had a shell that was relatively unfilled by larval tissues such as the digestive gland and gut (Figure 3b), and the velum was frequently small with a minimal propodium (Figure 3b).

Reciprocal Feeding Experiment

Both the northern intertidal and southern subtidal slugs showed less increase in growth on a diet of *Sertularia* spp. (Figure 4) than on *Obelia* spp. Although the starting lengths were similar for both trials, the final lengths were much higher for those fed *Obelia* spp. (Figures 4a, b) and the percent change in lengths was significantly higher for northern intertidal and southern subtidal individuals in this treatment. Similarly, the mean number of spawn masses produced per nudibranch was consistently less for all those fed *Sertularia* spp. (Figure 4d). The only significant differences for spawn mass output were found for the northern intertidal trial because of high levels of mortality in the southern subtidal treatment group (Figure 4d). Despite these differences in diet quality, all northern intertidal nudibranchs produced spawn masses yielding viable lecithotrophic veligers, and all southern subtidal *D. frondosus* had planktotrophic veligers. Once again, no mixed clutches were deposited. The characteristics presented earlier (Figure 3, Table 1) were used to distinguish these two larval types.

Mating Recognition Behavior

Adult *D. frondosus* from northern intertidal and southern subtidal habitats did not recognize each other as potential mates (Table 2). These slugs did not engage in copula even though others individuals collected at the same sites were actively mating (Table 2). Since only planktotrophic larvae were produced by *D. frondosus* from southern subtidal sites and only lecithotrophic larvae came from those at northern intertidal sites, these crosses reflect the two developmental types. Sperm storage from previous mates cannot be ruled out in these trials; therefore, these data do not evaluate fertilization success. These results only represent the potential for behavioral recognition of adult mates. The limited number of trials with *D. frondosus* from northern subtidal sites suggests that these individuals mate exclusively with either the northern intertidal or the southern subtidal adult nudibranchs. None of the four adults from the northern

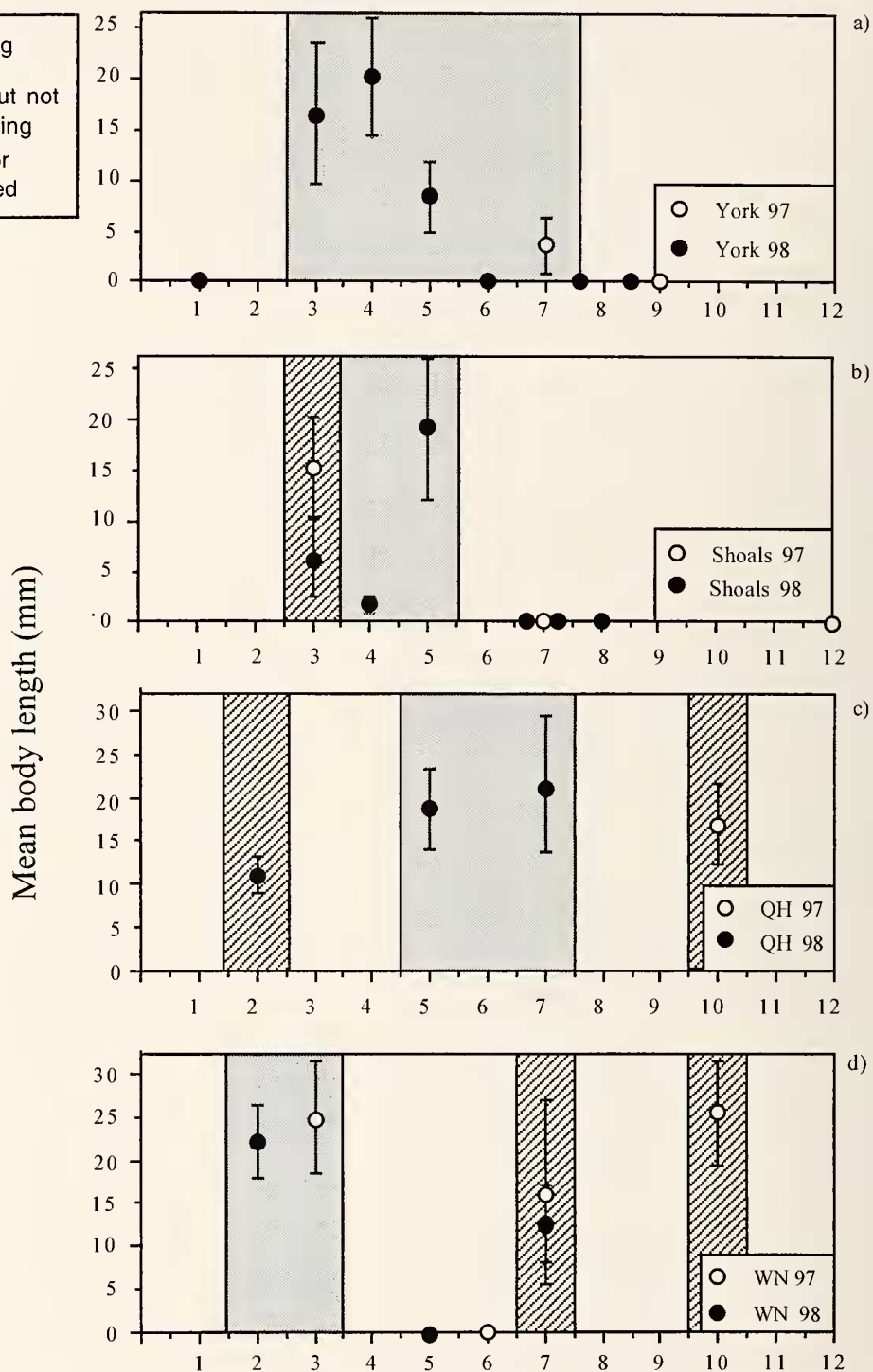


Figure 2. Mean body length (\pm standard deviation, $10 < n < 23$) of *D. frondosus* versus the month of collection in 1997 and 1998 (January = 1, December = 12). Southern subtidal sites are located at (a) Cape Neddick in York, Maine and (b) the Isles of Shoals, New Hampshire. Northern intertidal sites included (c) West Quoddy Head (QH), Maine, and (d) Wilbur Neck (WN) in Pembroke, Maine. Periods of spawning are shaded between consecutive months.

Table 1

Morphological and developmental characteristics for planktotrophic and lecithotrophic larvae collected in the Gulf of Maine. Included are the zygote diameter upon deposition, the maximum length of the larval shell and the embryonic capsular period from deposition through hatching. Values include means with the number sampled (n) \pm standard deviation. Zygote diameters ranged between 85–123 μm for planktotrophic larvae and 183–218 μm for lecithotrophic larvae. Feeding capacity was evaluated with micro-algae in laboratory culture conditions (see Methods).

Larval type	Zygote diameter (μm)	Capsular period (days)	Shell length (μm)	Feeding capacity
Planktotrophic	102 (70) \pm 12.2	6.7 (11) \pm 2.5	220 (19) \pm 23	Required
Lecithotrophic	194 (70) \pm 14.8	32 (22) \pm 8.9	310 (17) \pm 49	Incapable

subtidal sites would mate with nudibranchs from both of the other two habitats.

DISCUSSION

There are two disparate life history patterns for *D. frondosus* in the Gulf of Maine. These patterns are most evident at southern subtidal and northern intertidal sites,

while northern subtidal sites may represent overlapping populations between the two types. At southern subtidal sites, the irregular size distributions and timing of spawning events indicate that *D. frondosus* is a fast-growing, more opportunistic predator with a sub-annual seasonal distribution (Todd, 1981). The most common hydroid at these sites, *Obelia geniculata*, is extremely ephemeral and may be nearly exhausted by a combination of predators within only a few months (Lambert, 1991). In contrast, the consistent increase in length among northern intertidal populations of *D. frondosus* followed by a discrete spawning event (Figures 2c, d) indicates that these nudibranchs are relatively slow-growing with an annual seasonal distribution (Todd, 1981). The most common hydroid at these sites, *Sertularia pumila*, is present throughout the year, possibly supplying a constant source of food for these nudibranchs. The senescence of adults after a spawning period (Figures 2c, d) supports the idea of a discrete reproductive event, thus an annual life history pattern (Todd, 1981). The absence of nudibranchs at the Wilbur Neck site following the spawning period (Figure 2d) could be during a period when the larvae are in the water column or when newly recruited individuals are either too small to locate or in a microhabitat different than the adults. These habitats and patterns of feeding ecology have been outlined previously (Meyer, 1971; Clark, 1975; Lambert, 1991; Bleakney, 1996), but not in consideration of the two different larval feeding types produced in these populations and their general biogeographical distribution.

Larvae produced from animals collected at these sites had distinctly different characteristics corresponding with habitat and geographic location. *D. frondosus* produces obligate planktotrophic veliger larvae in southern and northern subtidal habitats. These larvae develop to hatching in a relatively short period of time (Table 1) and may have a longer dispersal potential, corresponding with the opportunistic, highly seasonal occurrence of adult populations. Lecithotrophic veliger larvae are produced by populations in northern intertidal and northern subtidal habitats, and show the potential for limited dispersal by metamorphosing in response to the egg mass jelly. This

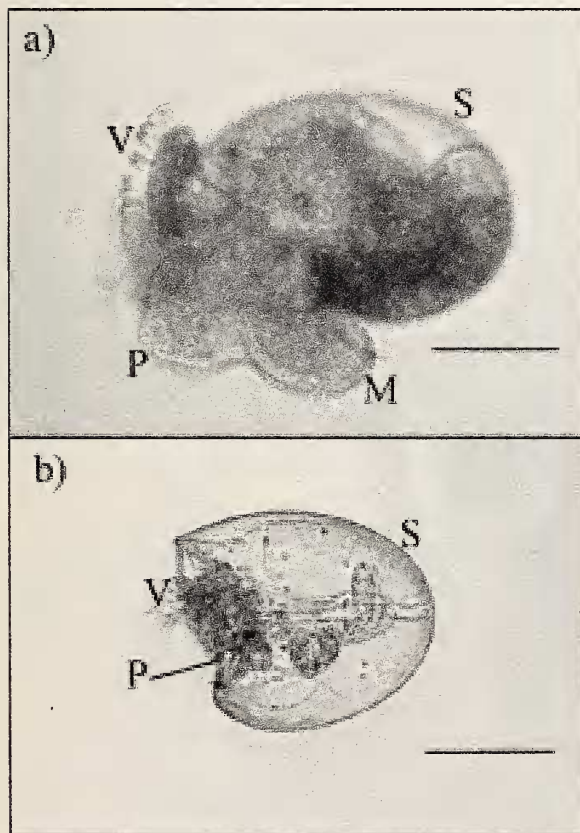


Figure 3. Light micrographs of *D. frondosus* larvae (bar = 100 μm). a. Lecithotrophic veliger larva from the northern Gulf of Maine. b. Planktotrophic veliger larva from the southern Gulf of Maine. S = shell, V = velum, P = propodium, M = metapodium.

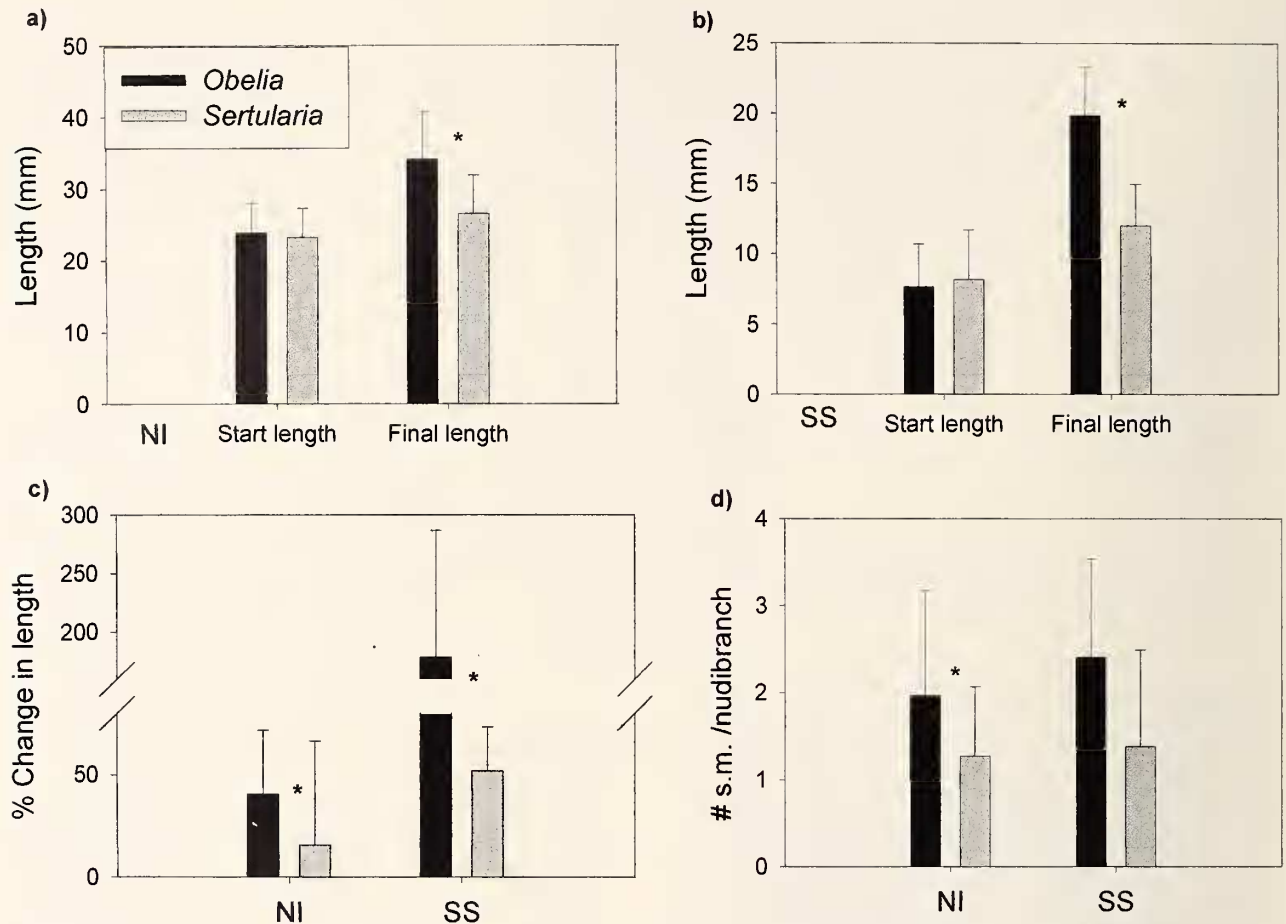


Figure 4. Results from reciprocal feeding experiment with *Obelia* sp. and *Sertularia* sp. fed to *D. frondosus* collected from northern intertidal (NI) and southern subtidal (SS) sites. All results are mean values (\pm standard deviation) and all comparisons are with a two-tailed t-test, except for the non-parametric Mann-Whitney test for spawn mass products. a. Starting ($n_{Obelia} = 30$, $n_{Sertularia} = 30$, $t = 0.545$, $df = 58$, $P = 0.59$) and finishing ($n_{Obelia} = 22$, $n_{Sertularia} = 29$, $t = 4.82$, $df = 49$, $P \ll 0.001$) lengths for NI trial. b. Starting ($n_{Obelia} = 25$, $n_{Sertularia} = 24$, $t = 0.533$, $df = 47$, $P = 0.60$) and finishing ($n_{Obelia} = 23$, $n_{Sertularia} = 12$, $t = 6.63$, $df = 33$, $P \ll 0.001$) lengths for SS trial. c. Percent change in length (change in length/initial length) for NI ($t = 3.72$, $df = 49$, $P < 0.001$) and SS ($t = 3.83$, $df = 33$, $P < 0.001$) trials. d. Mean number of spawn masses (s.m.)/nudibranch produced by individuals fed the two treatment diets for NI ($U = 235$, $P \ll 0.001$) and SS ($U = 9.0$, $P > 0.10$) trials.

Table 2

Results of mating recognition behavior crosses between *D. frondosus* from northern intertidal (NI) and southern subtidal (SS) sites. Northern intertidal adults always produced lecithotrophic larvae and southern subtidal adults always produced planktotrophic larvae. * Denotes significant difference ($G_c = 9.1$, $p < 0.05$). † Denotes significant difference ($G_c = 26.6$, $p < 0.05$).

Cross	Copulation observed	No copulation	Total # trials
NI \times NI*	8	10	18
NI \times SS*†	0	18	18
SS \times SS†	15	3	18

response is similar to that found for other opisthobranchs (Gibson & Chia, 1989; Chester, 1996) and although the ability to delay metamorphosis (Pechenik, 1990) may still exist, this limited dispersal potential corresponds with the year-round persistence of adults and may be adaptive for a seasonally constant food source.

Characteristics of egg size and capsular period directly correlate to larval feeding types among nudibranchs (Todd, 1981). Zygote diameters in this study were similar to published values for planktotrophic (Clark, 1975; Strathmann, 1987) and lecithotrophic veligers (Thompson, 1967) for *D. frondosus*. Capsular periods were also in the range of published values for planktotrophic (Hurst, 1967; Williams, 1971) and lecithotrophic (Thompson, 1967) *D. frondosus* veligers. No mixed clutches were